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EUROPEAN PLETHODONTIDS: PALAEONTOLOGICAL DATA AND BIOGEOGRAPHICAL CONSIDERATIONS

(AMPHIBIA)

INTRODUCTION

The family Plethodontidae offers one of the most fascinating and curious cases of biogeography. Although it is the caudate family with the highest number of representatives (more than half of the caudate species), plethodontids show a range that is almost entirely American, the only exception being the presence of some species in a limited area of Europe: south-eastern France, part of the Italian peninsula and Sardinia (Lanza *et alii* 1995; Gasc *et alii* 1997; Pough *et alii* 2001). The fact that European populations appear to be similar to some Californian species, and hence considered by some authors (among others Jackman *et alii* 1997; Pough *et alii* 2001) as belonging to the same genus (*Hydromantes* Gistel, 1848), makes the case even more curious deserving the definition written more than 20 years ago by Lanza & Vanni (1981): "the *Hydromantes* problem".

Even not taking into consideration the nomenclatural status of the European species, whether allocated to *Hydromantes* or to the genus *Speleomantes* Dubois, 1984 (see Dubois 1984, for details; Lanza *et alii* 1995; Societas Herpetologica Italica 1996; Razzetti *et alii* 2001), the solution of the biogeographic problem requires answers

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concerning the phylogenetic relationships of the European and Californian species, and, as all the authors agree in recognising a North American centre of dispersal for this family, when and how the spread toward Europe took place. Since an answer to such questions requires the collection of information concerning processes developed through time, it could be of some help to determine if the fossil record can furnish any clue.

RESULTS

As already noted by MILNER (2000), the caudate fossil record is palaeoecologically and taphonomically biased and the terrestrial and upland stream-dwellers of small size (as the plethodontids) are under represented. The fossil record of Cenozoic caudates is relatively poor if compared to that one of anurans and it is based mostly on remains of isolated vertebrae.

At present Europe is inhabited by members of four caudate families, Hynobiidae, Plethodontidae, Proteidae and Salamandridae (GASC *et alii* 1997), whose isolated trunk vertebrae are not difficult to allocate at order and family rank. In particular, plethodontids and salamandrids are the only ones with intravertebral exits of spinal nerves: vertebrae of these groups are therefore characterised by a distinct foramen opening on each side of the neural arch, at its base, caudal to the rib-bearers (EDWARDS 1976). Plethodontids can be distinguished from salamandrids since their vertebral bodies are amphicoelous and not opisthocoelous (ESTES 1981; MILNER 2000). Even not taking into consideration several other secondary characters, the presence of these foramina, as well as the centrum condition, are almost always detectable on fossil material (also on poorly preserved vertebrae) allowing an easy identification of plethodontids. Hence, it is rather surprising that the European fossil record is limited to the following 6 localities:

Locality	Region (Province) & Country	Age	References
Grotta Corbeddu, Oliena	Sardinia (NU), Italy	Late Pleistocene and Holocene	SONDAAR *et alii* 1984 and 1988; CALOI *et alii* 1986
Valdemino, Borgio-Verezzi	Liguria (SV), Italy	Middle Pleistocene	DELFINO 2002 and 2004
Grotte du Vallonnet	Alpes-Maritimes, France	Early Pleistocene	BAILON, pers. comm. (18-04-2002)
Monte Tuttavista, Orosei	Sardinia (NU), Italy	Plio-Pleistocene	DELFINO 2002; ABBAZZI *et alii* 2004
Siniscola	Sardinia (NU), Italy	undet. Pliocene (?)	LANZA *et alii* 1995
San Giovanni, Domusnovas	Sardinia (CA), Italy	undet. Pliocene (?)	LANZA *et alii* 1995

The most striking characteristic of these few data is that all the localities are relatively young in age (at least post Miocene; the remains of Siniscola and Domusnovas could be not Pliocene but Pleistocene in age) and limited in distribution within the modern range of the genus: 4 of them are on an island (Sardinia) and only 2 are from the mainland (Liguria -Italy- and Alpes-Maritimes -France).

Concerning the specific allocation of the remains, only those ones from Grotta Corbeddu have been referred at species rank: CALOI *et alii* (1986) identify them as *Speleomantes supramontis* (*Hydromantes supramontis* in the paper). However, this specific allocation does not seem to be grounded on morphology (a description is lacking) but only on the geographical provenience of the material, as Grotta Corbeddu is located in the *S. supramontis* range. Using a rigorous approach, it is therefore advisable to consider this datum simply at genus rank.

Although some features allowing a discrimination between the presently recognised 7 living European species have been described in the analysis performed by LANZA and co-workers (1995), they are not applicable to fossil remains that are usually represented by isolated vertebrae or, exceptionally, by disarticulated dentaries, maxillae and limb bones as in the case of the Monte Tuttavista sites (DELFINO 2002 and pers. obs.). The fossil remains of the European plethodontids are therefore not identifiable at species rank.

The fact that European fossils are relatively young, come exclusively from the present range and cannot be identified at species rank, makes them unsuitable for the determination of the route of dispersal from America to Europe and apparently useless in resolving the phylogenetic relationships of the modern taxa.

DISCUSSION

Several hypotheses have been put forward concerning the origin of European plethodontids. LANZA *et alii* (1995) thoroughly sum up the opinions of different authors grouping them into 3 categories: introduction by man, spread through a North Atlantic past connection and spread through the North Pacific Beringian Bridge (and then across the whole Asia). According to different authors, the timing of such spreads range from Cretaceous to Pliocene or even to Holocene if we consider the possibility of an introduction by man.

If the hypothesis of an anthropochorous origin can be easily excluded because European fossils predate the origin of mankind, it is rather difficult to evaluate the validity of the two other options.

The background information that should be taken into consideration to correctly confront this aspect of the "*Hydromantes* problem" can be summarised as follows:

- plethodontids probably originated in North America and should be at least 80 million years (Myr) old; their antiquity can be inferred by the sister-group relationships with the family Amphiumidae whose fossil record extends into the Upper Cretaceous (MILNER 2000);
- the fossil record of plethodontids is astonishingly poor and recent: not taking into account a single vertebra coming from the Lower Cretaceous of Spain, that showing intravertebral spinal foramina could belong either to the Plethodontoidea or the Ambystomatoidea clades; the oldest fossils come from the Lower Miocene of North America (Desmognathinae are known from the Pleistocene, Plethodontini from the Lower Miocene, Hemidactyliini from the Pleistocene and Bolitoglossini from the Upper Miocene of North America; MILNER 2000 and cited references);
- North America land continuity with Europe ended approximately

around 49 Myr ago, during the Lower Eocene (McKenna 1975 and cited references);

- North American permanent land continuity with Asia (through the Beringian Bridge) ended during the Neogene, probably already during the Miocene (Sher 1999; Marincovich & Gladenkov 1999);
- Europe had been isolated between the Lower Eocene and the beginning of the Oligocene not only from North America but also from Asia because of the presence of the Obik Sea and the Turgai Strait which extended from the Arctic Ocean to the Tethyan sea (McKenna 1975 and quoted references; for the effects of the closure of Turgai Strait on western European herpetofauna see Rage 1984, 1986);
- on allozyme and immunological basis, the separation between the Californian and European plethodontids has been assessed to be 28 Myr old (Wake *et alii* 1978);
- caudates cannot easily cross salt-water barriers being extremely sensible to osmotic variations.

The supporters of the "Beringian hypothesis" give credit to the assumed 28 Myr old separation between the Californian and European plethodontids. Since the Atlantic Ocean was already open at that time, the only available possibility for plethodontids to reach Europe was to spread through the Beringian Bridge and subsequently across Asia. The timing of the separation between the two lineages is not in conflict with the history of the Beringian Bridge. According to Sher (1999), Asia and North America "before the Neogene had constituted a single continent", that is to say that prior to 16-17 Myr plethodontids could have colonised Asia via the Bering Bridge. This is supposed to have happened to the anuran families of Bufonidae and Hylidae during the Oligocene (Borkin 1999 and quoted literature) or earlier. Although intermittent contacts took place during the Neogene and Quaternary, a late Neogene spread of plethodontids can be excluded not only because of possible unfavourable environmental conditions, but also because fossils indicate their presence in Sardinia during the Pliocene already.

On the other hand, LANZA *et alii* (1995) state that "it appears hardly credible that a whole family [...] disappeared from almost all of Europe and from all of Asia, or at least from all of Palearctic Asia, all the more so because wide proportions of the latter (SCHMIDT 1946) surely felt no or only slight effects of the Pleistocene glaciation". This objection seems to be so strong to deserve some comments. The "Beringian hypothesis" and a westward spread towards Europe could agree with the general trend that sees the post-Oligocene European herpetofauna, the amphibians in particular, as being largely a product of a westward expansion of Asian taxa, but in all the cases in which range shrinkage strongly affected Europe, there are invariably living survivors in south-eastern Europe or Asia (RAGE 1989, 1997; CHEYLAN 1995; SANCHIZ & ROCEK 1996; SANCHIZ 1997; BARBADILLO *et alii* 1997; IVANOV *et alii* 2000; DELFINO 2004). The latter continent seems to be an efficient faunal reservoir for Europe, that preserves living populations belonging not only to American herpetofaunal taxa that moved westward, through the Beringian Bridge, permanently colonising Europe (Bufonidae and Hylidae among anurans), or Asian taxa that temporarily extended their range into Europe (cryptobranchids and hynobiids among caudates), but also taxa that, although having probably originated in Europe, now survive in Asia only (the salamandrid members of the *Chelotriton-Tylototriton* group; CHEYLAN 1995; BORKIN 1999; VENCZEL 1999; MILNER 2000).

Assuming a spread via the Beringian Bridge, even if it is somehow acceptable that plethodontids did not leave fossil remains "while crossing" the entire Asia, it seems to be unlikely that this north American family, which undergo an extensive adaptive radiation in the New World tropics (WAKE 1987), did not leave any relict population in Asia.

Moreover, it is worth mentioning that there are cases, supported by fossil evidences, testifying that among caudates (cryptobranchids and salamandrids; MILNER 2000) faunal exchanges at the Beringian Bridge were directed from Asia to America but not the reverse.

LANZA and co-workers (1995) openly support dispersal of Europe via the "North Atlantic connection". Due to the ancientness of the last America-Europe direct connection, this hypothesis is incongruent with the supposed timing of split between the Californian and European species and their synapomorphies (see JACKMAN *et alii* 1997) that seem to require a more recent spread to Europe. However, NARDI *et alii* (2000), on the basis of DNA differences, contradict the idea of close relationships between Californian and European species confirming "that the European and American taxa represent two distantly related groups of species".

The objection recently moved by MILNER (2000) "As the bolitoglossines are restricted to western North America [...], it seems unlikely that they would have passed across eastern North America, and the developing Atlantic in the Early Cenozoic" is surprising since, the shortest way to reach southern Europe from the western North American coast is to cross the North Atlantic Bridge and not to face the whole of Asia. Moreover, if bolitoglossines originated in eastern North America (in the area now corresponding to the Appalachia) as suggested by WAKE (1966), the quoted objection looses its meaning.

The hypothesis that plethodontids could have reached Europe via the shortest way along with several other vertebrate taxa (McKENNA 1975; WEBB 1985; BRIGGS 1987) during the early-middle Palaeogene seems to be much more reasonable. Among the pre-Oligocene (that is to say before the closure of the Turgai Strait) small-sized herpetofauna there are several examples of taxa that spread from North America to Europe. It could be the case of the caudate family Dicamptodontidae that is now represented by a single genus in western North America but, according to some authors (ESTES 1981; ROCEK 1994), had representatives in Europe during the Palaeocene and Miocene (MILNER 2000, criticised the allocation of the European fossils to this family and considered them as enigmatic forms of uncertain position). Among anurans, a member of the American family Leptodactylidae has been found in the Upper (and possibly Lower) Eocene of Europe (see references in: SANCHIZ 1998; RAGE & ROCEK 2003). Among squamates, lizards of the families Helodermatidae and (perhaps) Necrosauridae reached directly Europe from North America (RAGE & AUGE 1994) while the Eocene snake fauna of Europe is so rich of American representatives that has been defined as "euro-american" (see IVANOV *et alii* 2000 and quoted literature).

The hypothesis of dispersal through the American-European connection requires a prolonged survival in Europe without any relevant morphological change or with a marked parallel evolution (among plethodontids "parallelism and convergence are rampant"; WAKE 1987). Although surprising, this prolonged survival is not so extraordinary considering that fossils of the living genus *Necturus* (a proteid whose closest relative, *Proteus*, lives in southern Europe) have been identified in the Palaeocene of North America (MILNER 2000), and caudates are known to be morphologically conservative (among others, JOCKUSCH & WAKE 2002).

Concerning the origin of the modern European species, some considerations could be further developed. According to NARDI *et alii* (2000; see also STEFANI 1969, and LANZA *et alii* 1995, for details), molecular systematic, electrophoretic and morphological data support the antiquity of the south-western Sardinian species *Speleomantes genei* (Temminck & Schlegel, 1838). Moreover, this species is the only one in which male digamety doesn't occur, and that is not parasitised by the taxa that eastern Sardinian and mainland species share (see literature in LANZA *et alii* 1995). It could be hypothesised that *S. genei* (or its forerunner) entered Sardinia from the Pyrenees (or south-western France) before the migration of the Corso-Sardinian microplate (migration referred to the Late Oligocene-Early Miocene; ALVAREZ 1972; MONTIGNY *et alii* 1981); the same authors, as well as LANZA *et alii* (1995) and NASCETTI *et alii* (1996) suggest that the eastern Sardinian species could have colonised the island coming from the Italian peninsula during the Late Miocene (Messinian) salinity crisis. The first hypothesis is consistent with what already supported by CACCONE *et alii* (1994) for another caudate genus, genus *Euproctus* Gené, that entered the microplate before its rotation and that still survives in both islands as well as in the Pyrenean region. For parsimony reasons, and taking into consideration the well known conservative power of islands (MASINI *et alii* 2002), the second hypothesis could be modified in the sense that *S. genei*, or its forerunner, entered Sardinia in Oligocene, survived there while mainland (at least Pyrenean) populations went extinct, giving rise to the rest of the Sardinian species (3) which are responsible of the further spread into Peninsular Italy (3 species). This evolutionary scenario has been already suggested by LA GRECA (1984), partly modifying the ideas of STEFANI (1969) who supposed that *S. genei* originated both the eastern Sardinian species and the continental ones (from an ancient stock that reached the Maritime Alps). The origin of the continental species from the eastern Sardinian ones, rejected by NASCETTI *et alii* (1996) because "not supported by the present patterns of geographic distribution", is simply speculative at the moment, and the mode and timing of the speciation process still have to be defined (but see FROMHAGE *et alii* 2004, for a similar pattern of dispersal in *Discoglossus*).

It would fit the antiquity of *S. genei*, its lower genetic distance from the other Sardinian species than from the continental ones (LANZA *et alii* 1995: 240; NASCETTI *et alii* 1996: table 3 and 5) and, above all, it would better explain the fact that European fossils are found only inside the present range and mostly in Sardinia (where they are not rare!), a fact suggesting relatively recent expansion of the range on mainland Italy and France. Moreover, molecular data indicate that the separation (from each other) of the modern eastern Sardinian species dates back to the Late Pliocene (CIMMARUTA *et alii* 1998; note that *S. flavus*, the northern species -farthest from *S. genei*- is relatively more differentiated than the others), while the separation (from each other) of the continental species is more recent and seems to be Early Pleistocene in age (FORTI *et alii* 1998).

CONCLUSIONS

The "*Hydromantes* problem" does not seem to show any clear solution. The paucity of fossil remains in both America and Europe does not allow one to directly find a plausible solution to the problem, leading to speculations based on contrasting data which are inferred mainly from biogeography and molecular biology, whose evolutionary weight has not been unambiguously assessed yet.

Under a parsimony approach, assuming a long-term conservation of some traits, it seems more likely that the ancestors on the European taxa spread eastward across the North Atlantic land continuity, rather than westward across the Beringian Bridge and the whole Asia.

In any case, it is possible to predict that outside the modern range of *Speleomantes*, the Pyrenean area is the one which surely can provide fossils of plethodontids.

Furthermore, it is tempting to suggest that the continental species of Europe derive from the eastern Sardinian ones and not the reverse.

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ABSTRACT

The European fossil record of plethodontids is surprisingly poor (only 6 post-Miocene localities) if one considers that it is rather easy to identify their remains among those of the other caudates that inhabited Europe during the Cenozoic. The facts that European fossils are relatively young, come exclusively from the present range and cannot be identified at species rank, makes them unsuitable to determine the direction of dispersal of Europe from America and apparently useless in resolving the phylogenetic relationships of the modern taxa. Although it is not possible to assess unambiguously the evolutionary weight of contrasting data inferred from biogeography and molecular biology, the absence of relict Asian populations can be interpreted to suggest that a direct spread preceding the separation of Europe and North America (along with the well known mammal and herpetofaunal dispersal) is less unlikely than a dispersal requiring the crossing of the Beringian Bridge and the whole of Asia. There are also reasons to suggest that the continental species of Europe could derive from the eastern Sardinian ones and not the reverse.

RIASSUNTO

Pletodontidi europei: dati paleontologici e considerazioni biogeografiche (Amphibia).

Sebbene sia relativamente semplice riconoscere i resti fossili dei membri della famiglia Plethodontidae da quelli delle altre famiglie di caudati che hanno abitato l'Europa durante il Cenozoico, il loro registro fossile è limitato a 6 località, di cui 5 italiane (4 in Sardegna e 1 in Liguria) e 1 francese (Alpes-Maritimes), non più antiche del Pliocene e localizzate all'interno dell'attuale areale. Inoltre, l'assenza di fossili provenienti dall'Asia e la scarsità di quelli nordamericani (i più antichi risalgono al Miocene inferiore) ostacolano la formulazione di teorie che consentano di spiegare come si siano originati i popolamenti europei di una famiglia altrimenti essenzialmente americana. Inoltre, non è possibile valutare in modo inequivocabile il peso dei molti e contrastanti dati di carattere biogeografico e molecolare. Alcune considerazioni di carattere bio- e paleobiogeografico, fra cui l'assenza di popolazioni relitte di pletodontidi in Asia, sembrano però suggerire che una diffusione verso est (quindi diretta), sulla scia di ben documentate dispersioni faunistiche che hanno interessato sia la mammalofauna sia l'erpetofauna, e precedente alla separazione del Nord America dall'Europa, sia più probabile di una diffusione che richieda l'attraversamento del ponte di Bering e di tutta l'Asia. Inoltre, la possibilità che le specie dell'Europa continentale derivino da quelle della Sardegna orientale sembra l'ipotesi più plausibile.

NOTE ADDED IN PROOFS

An unexpected Plethodontid caudate has been recently found in the Middle Miocene of Slovakia (VENCZEL & SANCHIZ, 2005). This datum widens considerably the past European range of the family but seems not to be sharply in contrast with any of the biogeographical scenarios here reviewed or proposed.

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